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Amanita magniverrucata—revision of an interesting species of *Amanita* section *Lepidella*

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This paper is dedicated to DR. CORNELIS BAS
on the occasion of the fortieth anniversary of the publication of
his groundbreaking thesis on *Amanita* and its section *Lepidella*.

Abstract—A revision is provided for *Amanita magniverrucata*, a species known from the state of California, USA, and reported from northern Baja California, Mexico. The universal veil appears to arise from the pileus context—without interposal of a pileipellis. The appropriate placement of *A. magniverrucata* in Bas' systematic scheme for *A.* sect. *Lepidella* is open to question. If the inflated cells of the volva are judged to be insufficiently elongate for placement in *Amanita* subsect. *Vittadiniae*, then a possible placement could be in *A.* subsect. *Solitariae*, within Bas' stirps *Microlepis*, in which the present species exhibits only limited phenetic similarity to previously assigned taxa. The present species may not be accommodated in the set of stirpes currently proposed for sect. *Lepidella*.

Key words—*Amanitaceae*, *Limacella*, North America, taxonomy.

Introduction

This paper is a continuation of taxonomic work on material of *Amanita* from the Pacific coastal regions of southwestern Canada, the Pacific coastal states of the USA, and northern Baja California. Previous papers on *Amanita* taxa of the same region have dealt with a revision (Tulloss & Lindgren 1992) of *A. smithiana* Bas (1969) and the proposal of two new taxa—*A. novinupta* Tulloss & J. Lindgr. (1994) and *A. aprica* J. Lindgr. & Tulloss (Tulloss & Lindgren 2005). Type studies of several regional taxa appear in (Tulloss 1994).

During revision of material of *A. magniverrucata*, it was noted that the universal veil appears to arise from the context of the pileus—without interposal of a pileipellis. This differs from the original interpretation of the same tissues in the species' protolog and subsequent publications, e.g., (Thiers 1982). This article focuses on morphological revision of *A. magniverrucata* and lays out concerns regarding its taxonomic placement.

Methods and materials

Methods used are those described, e.g., in (Tulloss 2000, 2008a).

(Kornerup & Wanscher 1978) is the source of color codes in the form of the following example: "4A6." Color names with first letters of words capitalized are from (Ridgway 1912). Munsell color notations (Anon. 1975) are in the form of the following example: 8.5YR 5.5/7.0. Munsell notational equivalents for Ridgway's names follow Hamly (1949).

Herbarium name abbreviations are conformant with (Holmgren et al. 1990), with the exception of "RET" (the author's herbarium).

Abbreviations in author citations follow Kirk & Ansell (1992, 2008).

Taxonomic part

Amanita magniverrucata Thiers & Ammirati, 1982. Mycotaxon 15: 161. **Figs. 1–3**

=*Amanita strobiliformis sensu* Arora, 1979. Mushr. Demyst.: 236, illus.
Illus.: Thiers, 1982. *Amanitaceae*. Agaricales Calif.: pl. 29A.
Illus.: Arora, 1986. Mushr. Demyst., 2nd ed.: 274 & pl. 55.
Illus.: Jenkins, 1986. *Amanita* N. Amer.: fig. 85.
Illus.: Phillips, 1991. Mushr. N. Amer.: 23.
Illus.: Tulloss, 2008c. *Amanita magniverrucata*. in Tulloss & Yang, eds., Studies gen. *Amanita* Pers.

PILEUS: 60–156 mm wide, white to whitish at first, darkening slightly when bruised, becoming sordid yellowish-cream with gelatinization in senility, globose to convex becoming plano-convex to plane or shallowly depressed in age, with surface having dry dull appearance until age, then moist to subviscid in senility or if universal veil fissuring extending into context, with visible color that of universal veil at first, context sometimes visible in senility, lacking distinct pileipellis; *context* 8–30 mm thick at stipe, thinning evenly to margin, white, unchanging when cut or bruised, firm; *margin* nonstriate, strongly incurved at first, decurved at maturity, often strongly appendiculate (with flocculence from universal veil on marginal region and with substantial (often subpolygonal) pieces of partial veil); *universal veil* at first as thick and rather smooth covering of entire pileus, then becoming areolate, later as conspicuous pyramidal warts, large over disc and much of pileus at first, smaller or absent toward margins (even at first), fleshy, with surfaces longitudinally striatulate, further stretching and flattened or breaking up with further pileus expansion, white to tan to light brown (5–7D4–8) to Warm Buff (1Y7.8/6.0), becoming darker brown to reddish brown on tips, sometimes becoming brownish to pale

reddish brown (below brown tips) from disc outward, up to 20 mm wide at base and 10 mm high, adnate until age (but rather easily broken and then leaving irregular scar on remaining universal veil tissue), detersile in senility due to rather thick region of gelatinization apparently including both wart bases and upper pileus context (observed in Pastorino 1-21-05E).

LAMELLAE: narrowly adnate or shallowly notched at first, becoming free, with decurrent line on stipe at least until loss of partial veil material, subdistant to crowded, white to off-white to pale ivory to pale buff, 9± mm broad, with fimbriate margin, often with partial veil remnants attached, broadest at about 75% of distance from stipe to pileus margin; *lamellulae* subattenuate, unevenly distributed, of diverse lengths, plentiful.

STIPE: 28–120 × 10–34 mm, white to whitish, often with brown to reddish brown to buff stains, cylindric to subcylindric or narrowing upward, not flaring at apex, dry, glabrous above partial veil, appressed fibrillose to flocculose below, eventually becoming longitudinally striatulate at least in part; *bulb* 35–105 × 18–60 mm, dauciform or napiform at first (about equal in width to developing pileus in some "button" specimens), becoming less strongly differentiated from stipe as both diameters decrease during expansion of stipe, often with shallow vertical splitting in upper half, sometimes doglegged; *context* white, unchanging when cut or bruised, solid, dense; *partial veil* apical to superior, eventually breaking and tearing and (subsequently) lost or collapsing on stipe, white, submembranous to subfelted to floccose-fibrillose, with plentiful soft white cottony patches on underside; *universal veil* as scattered warts on stipe below partial veil and as one to 11 or more irregular or concentric rings (entire or comprising scales or warts) on upper bulb and lower stipe, white, becoming brownish or orange-brown with age, friable, often disappearing with age.

Odor indistinct at first, later strong and unpleasant. *Taste* mild.

MACROCHEMICAL TESTS: $FeSO_4$ - greenish then gray on pileus context (protologue). Spot test for tyrosinase (paracresol) - only minor reactions in bulb in "button" specimen. Spot test for laccase (syringaldazine) - negative throughout basidiome. [Chemical test voucher for phenoloxidases: Tulloss 11-24-89-D.]

PILEIPELLIS: poorly differentiated or absent. PILEUS CONTEXT: filamentous, undifferentiated hyphae 2.5–17.5 µm wide, branching, plentiful to dominating, curving, interwoven or tangled loosely, without dominant orientation, with thin to slightly thickened walls, sometimes with yellowish subrefractive walls; acrophysalides plentiful, clavate to fusiform to ellipsoid to ovoid to subpyriform, up to 85 × 38 µm or larger; vascular hyphae 3.8–16.8 µm wide,

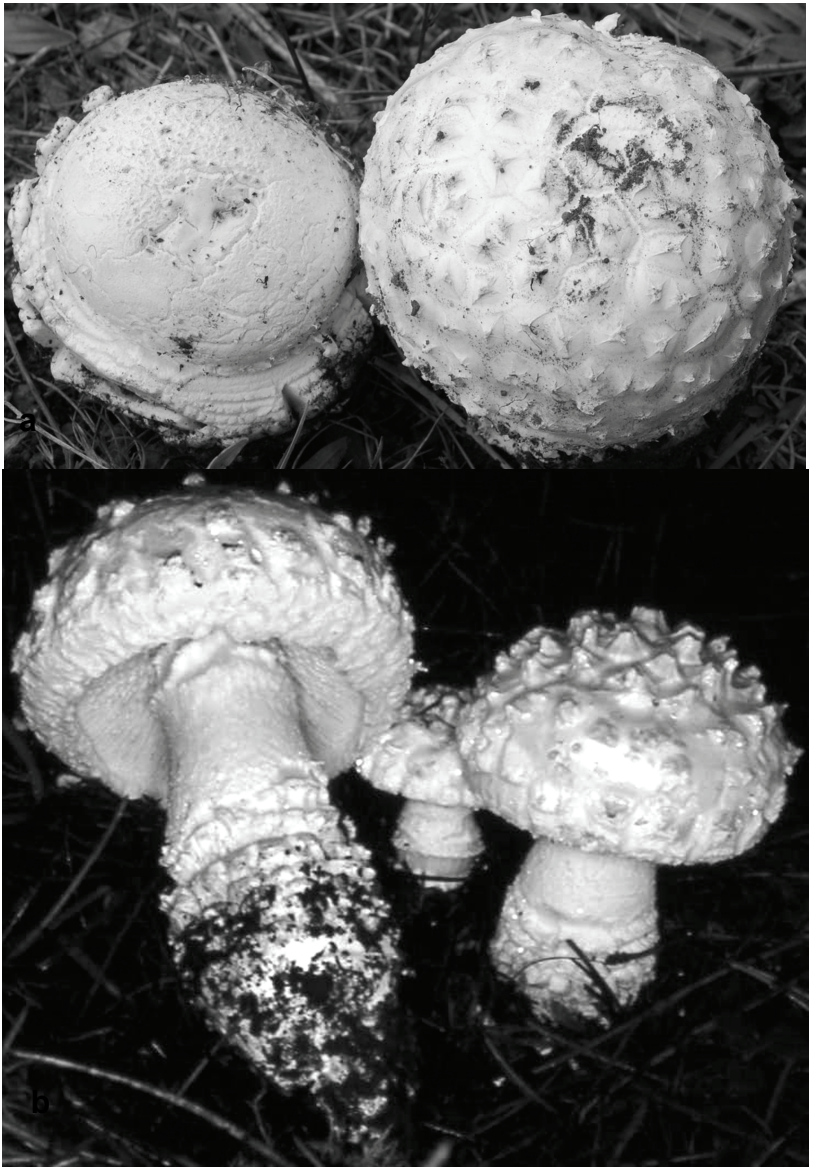

Fig. 1. *Amanita magniverrucata*, habit. a. Buttons in early stage of expansion. Photogr. by D. Bojantchev (off Mt. Vision Rd., Point Reyes, Calif., elev. 200 m, with *Pinus muricata*, *Arctostaphylos manzanita*, and *Vaccinium ovatum)*. < http://mushroomhobby.com/Gallery/Amanita/index.htm#Amanita_magniverrucata >. b. Expanded, but immature, specimens. Photogr. by R. Pastorino (with *P. muricata*, 21.i.2003 R. Pastorino s.n.)

Fig. 2. *Amanita magniverrucata*, habit, mature specimens (with *Pinus muricata* [not depicted], ca. Skyline Dr., Oakland, Calif., 9.ii.2003). Photograph by D. L. Viess.

branching, yellow-brown, scattered, locally common. LAMELLA TRAMA: bilateral; w_{cs} = 75–115 µm; with elements of subhymenial base [uninflated

and partially inflated hyphal segments and intercalary clavate cells (e.g., 32 × 16.5 µm, 41 × 15.0 µm)] diverging at angles up to 45° and concatenated in sweeping curve to subhymenium; filamentous, undifferentiated hyphae 3.2–11.0 µm wide, branching, with constrictions at some septa, with some intercalary segments slightly inflated; divergent, terminal inflated cells absent(?); vascular hyphae not observed; clamps infrequent. SUBHYMENIUM: w_{st}-near = 80–110 µm; w_{st}-far = 110–150 µm; comprising a branching structure of inflated cells (subglobose to pyriform nearest to subhymenial base and fusiform nearest basidia) and short uninflated hyphal segments, with elements having major diameter perpendicular to the central stratum for at least two cell lengths below bases of longest basidia, with basidia arising from uninflated or partially inflated hyphal segments or fusiform cells or very small subglobose inflated cells or branched elements (with varying degrees of inflation), with 2 to 2½ cells between bases of shortest and longest basidia; clamps infrequent. BASIDIA: 28–52 × 7.0–11.8 µm, thin-walled, dominantly 4-, but also occasionally 2- or 1-sterigmate; clamps and proliferated clamps infrequent, sometimes thin-walled and inconspicuous. UNIVERSAL VEIL: On pileus: with orientation of elements dominantly periclinal in base of wart but anticlinal or periclinal in upper part, with elements of lower part of wart dominantly hyaline and colorless and (at very base) arising from hyphae of dense upper portion of pileus context; with elements of upper part yellow-brown to orange-brown in mass (individually clouded and sordid yellowish to yellow to yellow-brown) and gelatinizing and somewhat disordered; filamentous, undifferentiated hyphae 3.5–19.5 µm wide, branching, common, occasionally with yellowish subrefractive walls, with those segments or parts of segments of largest diameter having slightly thickened walls; inflated cells dominating, terminal, singly or in short chains, with cells in such chains often easily dissociating, subglobose to ellipsoid to ovoid to clavate to broadly fusiform or subcylindric (with latter two forms the least common and restricted to smaller cells), up to 76 × 56 µm, with walls 0.5–1.0$^+$ µm thick; vascular hyphae 4.0–12.2 µm wide, sometimes brownish yellow, branching, unevenly distributed, locally common; clamps thin-walled, inconspicuous, infrequent. On stipe base, at top of bulb in immature specimen: very similar to material on pileus, with greater proportion of filamentous, undifferentiated hyphae, with some inflated cells brown, with inflated cells smaller (on average) than on pileus. STIPE CONTEXT: longitudinally acrophysalidic; filamentous, undifferentiated hyphae 1.8–11.0 µm wide, plentiful, branching, often in longitudinally oriented fascicles, occasionally with yellowish subrefractive walls, with walls thin or up to 1.0 µm thick; acrophysalides dominating, up to 203 × 55$^+$ µm, with walls thin or up to 0.5 µm thick; vascular hyphae not observed. PARTIAL

VEIL: filamentous, undifferentiated hyphae 3.2–8.0 µm wide, dominating, frequently branching, twisting and coiling, often in fascicles of rather few hyphae, sometimes with yellowish subrefractive walls, with walls thin to slightly thickened; inflated cells scattered, occurring more frequently in region adjacent to stipe surface, clavate, terminal (singly), up to 51 × 11.5 µm (but often about 60% of this size or less), with walls slightly thickened or up to 0.5 µm thick; vascular hyphae 6.0–9.0 µm wide, infrequent.

BASIDIOSPORES: [260/12/10] (6.5–) 8.0–12.6 (–15.5) × (4.5–) 5.8–8.0 (–9.5) µm, (**L** = 8.5–11.6 (–12.0) µm; **L'** = 10.3 µm; **W** = 6.0–7.4 (–7.5) µm; **W'** = 6.8 µm; Q = (1.17–) 1.31–1.79 (–3.75); **Q** = (1.39–) 1.41–1.66; **Q'** = 1.52), hyaline, colorless, thin-walled, smooth, amyloid, ellipsoid to elongate, rarely bacilliform or irregularly shaped in specimens with sporulation just beginning when dried, adaxially flattened, sometimes inflated at one end; apiculus sublateral, cylindric; contents mono- to multiguttulate; white in deposit.

ECOLOGY: Solitary to gregarious, apparently uncommon in some years throughout its range, but sometimes producing common fruitings (protolog). California: In coastal forests, with *Pinus muricata* D. Don and *Quercus agrifolia* Née or with *Quercus* and *Arbutus menziesii* Pursh or with *P. muricata* and *Arctostaphylos manzanita* Parry and *Vaccinium ovatum* Pursh or in dark loam under conifers. Possibly associated with similar trees in Baja California Norte, Mexico.

With regard to recovery after forest fire, the following was received from T.D. Bruns (UBC) (pers. comm., 10.vi.2008): "The ... [*A. magniverrucata* collecting] location on Limantour Rd in Pt Reyes burned in 1995, and the species disappeared from the site for over a decade. But this year we got several collections of it from the area again."

MATERIAL EXAMINED: **USA**: CALIFORNIA—Alameda Co. - Oakland, ca. Skyline Blvd., 20.i.2003 Mark Lockaby s.n. [Tulloss 1-20-03-A] (RET), 31.i.2003 Debbie Viess s.n. (RET). Marin Co. - ca. Bon Tempe Lk., 21.i.2005 Ron Pastorino 1-21-05E[1] (RET); Inverness Ridge, Chris Thayer & Phil Baird s.n. [Tulloss 11-24-89-D] (RET); Tomales Bay St. Pk., 21.i.2003 R. Pastorino s.n. (RET). Mendocino Co. - Mendocino, xi.1991 D. Arora 2001 (RET) & 2002 (RET). Santa Barbara Co. - Montecito, E. Valley Rd., 12.ii.1950 M. G. Rea F.11 (MICH); no locale, 21.iii.1944 P. M. Rea H.1341 (MICH). Santa Cruz Co. - Santa Cruz, 19.iii.1987 Marsha Heidt s.n. [H. D. Thiers 51203] (SFSU). San Mateo Co. - San Francisco Watershed, 13.iii.1970 Robert S. Keller 801 (SFSU, holotype; NY, isotype (n.v.)).

NOTES: This species was placed in *A.* sect. *Lepidella* when originally published; and, so far as I know, all subsequent authors treating the species have agreed (e.g., see the listed sources of illustrations, above). Within the cited

1. Collected as "button" and opened in vitro.

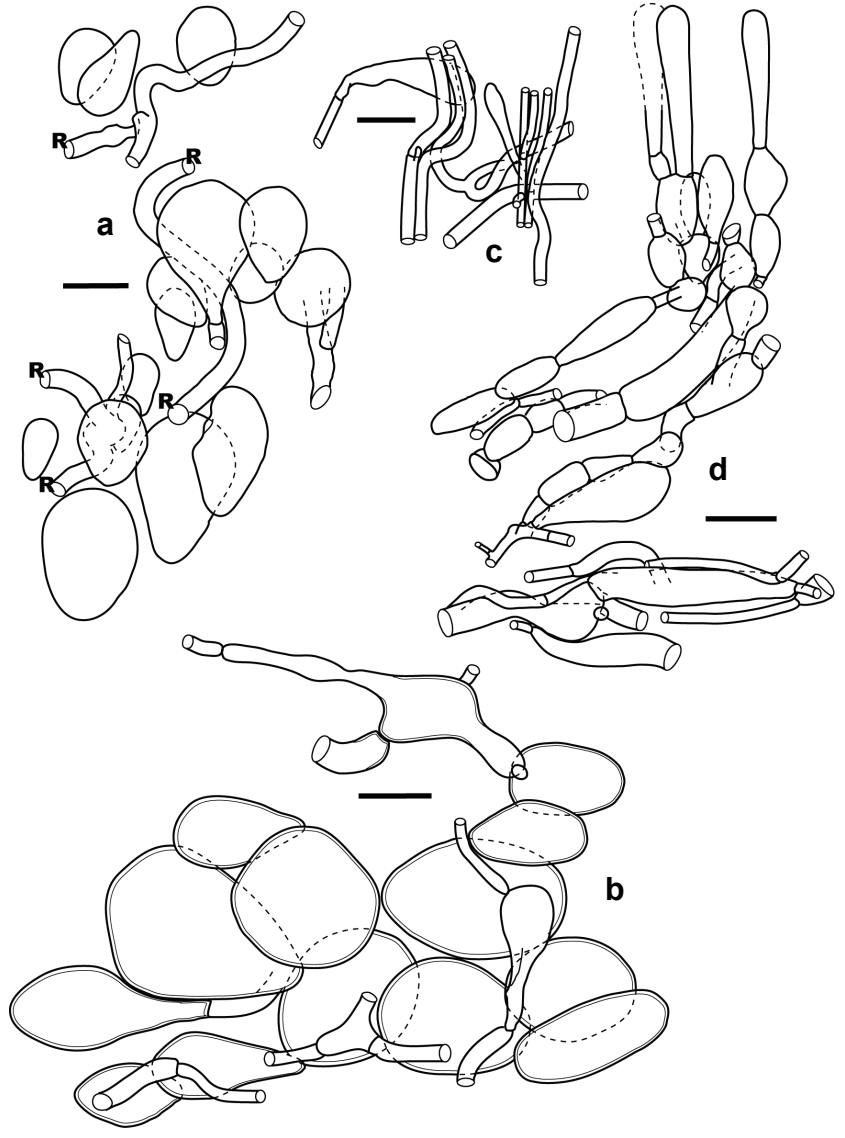

Fig. 3. *Amanita magniverrucata.* (a) Elements of universal veil on pileus, near exterior surface, thin-walled cells and anticlinal alignment (Tulloss 11-24-89-D). (b) Elements of universal veil from near base of wart, thickened cell walls and periclinal alignment (Thiers 51203). (c) Elements of partial veil (Thiers 51203). (d) Elements of hymenium, subhymenium, subhymenial base, and central stratum (Thiers 51203). "R" indicates an "end" of a refractive hypha. Scale bars = 20 μm.

section, placement in lower supraspecific ranks has not been attempted to the author's knowledge.

The protolog includes an apparent misinterpretation of the upper, denser part of the pileus context as a pileipellis, which was compounded by Thiers (1982: 29) who wrote: "pileus cuticle a trichodermium with terminal hyphal cells large and sausage shaped." While the description of the hyphae and acrophysalides are as in the protolog, the addition of the term "trichodermium" indicates that Thiers may have misinterpreted as a pileipellis that portion of the volva that often continues below the bottoms of the fissures that separate the warts.

By Bas' key (Bas 1969: 345), the present taxon could be placed in either *A.* subsect. *Solitariae* Bas (1969) or in *A.* subsect. *Vittadiniae* Bas (1969)—according to one's interpretation of the shape of the inflated cells of the volva. Other possibilities are eliminated because of (e.g.) the absence of an exterior, membranous layer in the universal veil of *A. magniverrucata*.

Placement within subsect. *Vittadiniae* would require interpretation of the basal cells of the volva as elongated and organized in chains. No other species in the subsection has cells of the shape illustrated in Fig. 3b. The absence of a pileipellis is very common (if not universal) in the known species of subsect. *Vittadiniae.* On the other hand, a scattering of taxa in other of Bas' subsections of *A.* sect. *Lepidella* also lack a pileipellis (see below).

The key to the stirpes within subsect. *Solitariae* (Bas 1969: 386–388) first requires knowledge of the presence or absence of clamp connections. Since, clamp connections were observed in multiple tissues of the material examined for this article, we are led to the choice of stirps *Microlepis* because the universal veil warts of the present species lack a "pad" dominated by hyphae at their bases and have their elements anticlinally oriented—at least in the upper portions of a wart..

One species placed by Bas (1969) within stirps *Microlepis* is of particular interest in terms of comparison to the present taxon—*A. abrupta* Peck (1897). This species' stipe has a subabrupt, napiform or turbinate bulb with continuous or occasionally broken, often rather finely delineated, concentric rings of universal veil tissue on its upper surface, somewhat mirroring the coarser concentric rings of volval material on the upper bulb of *A. magniverrucata.* The pyramidal, volval warts on the pileus of *A. abrupta* are much the largest of any of the other taxa Bas placed in stirps *Microlepis*. These pyramidal warts are (at first) connected to a pileipellis as little as 30 µm thick and lacking a noticeable, gelatinized suprapellis. *Amanita abrupta* differs from *A. magniverrucata* by having a distinct separation of universal veil from pileus context,

having notably more rapid loss of volval warts due to eventual gelatinization at the surface of the limited pileipellis, having a membranous and persistent partial veil, having smaller globose to subglobose spores, having surface fibrils of the stipe that are drawn upward (suggesting a cortina) on the underside of the partial veil, having a distribution limited to the eastern US, having an unusually strong and pervasive positive reaction to the syringaldazine spot test for the presence of laccase, etc. *Amanita sphaerobulbosa* Hongo (1969) is an east Asian taxon that appears to be quite similar to *A. abrupta*. Maintaining distinction between the two species is recommended by Yang & Doi (1999)—a position supported by the present author. *Amanita magniverrucata* is distinct from *A. sphaerobulbosa* by an argument similar to the one applied in the case of *A. abrupta*, above.

Arguments for either of the possible placements would require suppositions that do not seem entirely justified. The present species may be sufficiently unique to fail to fit into any of the stirpes Bas described. It seems preferable to await further evidence, perhaps from molecular studies.

The report of the present species from Mexico (Ayala et al. 1988) should be reinvestigated. The pileus on the material from Baja California is described as subviscid, the pyramidal warts are described as only 1 mm high (possibly a typographical error?), the partial veil is described as membranous, and the concentric rings of universal veil on the stipe's bulb are described as floccose.

In southern California, it may be possible to mistake *A. magniverrucata* for *A. subcaligata* (A.H. Sm. & P.M. Rea) A.H. Sm. ex Tulloss (Volk & Burdsall 1995) [=*A. salmonea* Thiers (1957) (Bas 1969: 360–361, figs. 45–47; Tulloss 2008b)] or vice versa because some specimens of the latter can have rather large warts on the pileus and many specimens have pinkish, orangish or rusty coloration, sometimes bruising to buff. However, *A. subcaligata* is clearly a species of *A.* subsect. *Vittadiniae* and can be distinguished from the present species by its having plentiful, concatenated, elongate inflated cells in the universal veil on the pileus.

Other taxa of section *Lepidella* that lack a well-formed pileipellis, are not assignable to subsect. *Vittadiniae*, and can easily be distinguished from the present taxon by Bas' keys (Bas 1969) include *A. rhoadsii* (Murrill) Murrill (1939) and *A. crassiconus* Bas nom. prov. (1969).

While a number of the new species described by Thiers & Ammirati (1982) originally were treated provisionally in unpublished MSc theses of Breckon (1968) and Nakamura (1965), the present species was not.

The present taxon has been called *A.* species C15 and *A.* species Vitt4 by the present author in old versions of regional keys and correspondence.

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